

## A Canopy Transpiration and Photosynthesis Model for Evaluating Simple Crop Productivity Models

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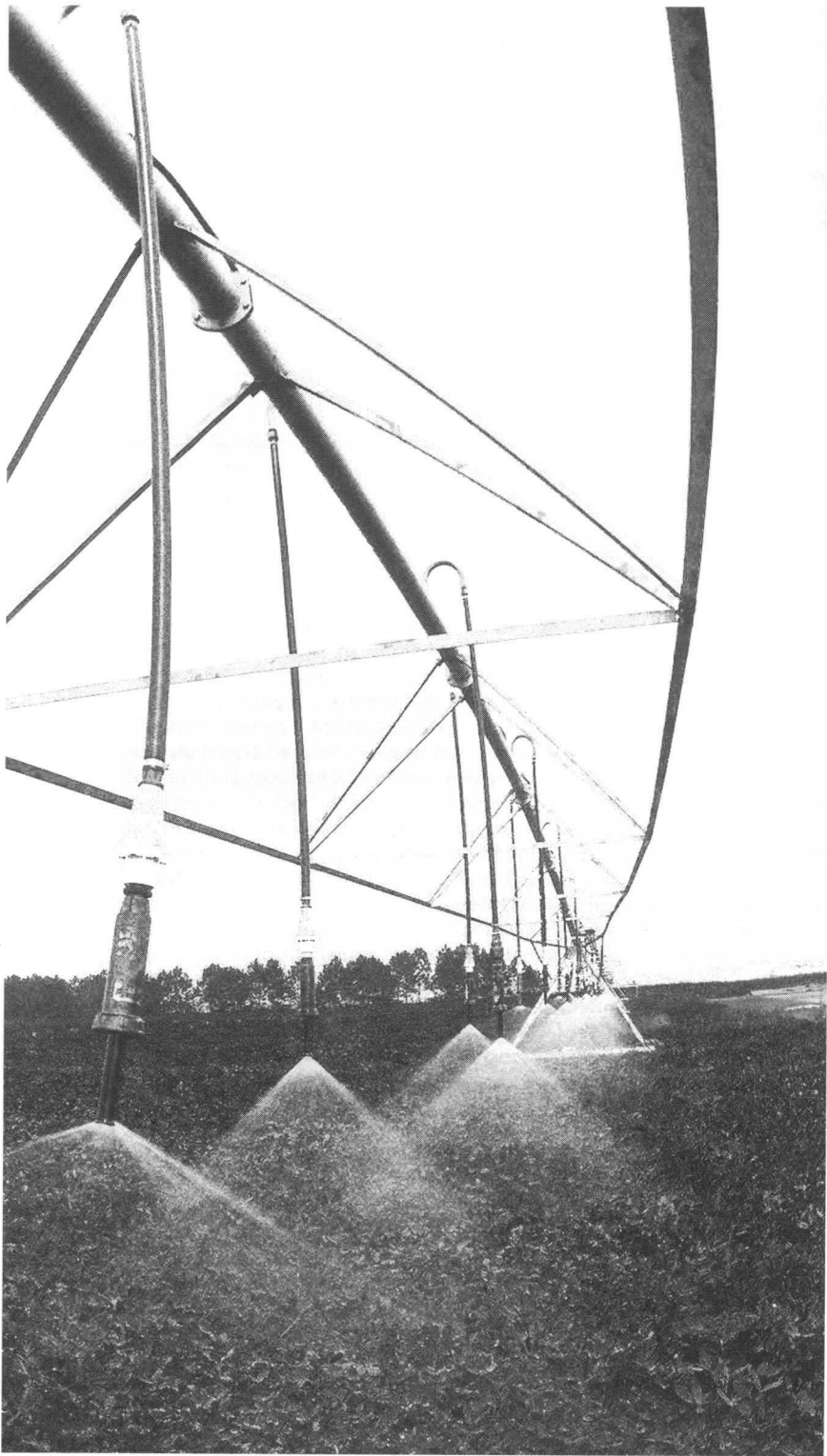
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### Abstract

There has been a renewed interest in evaluating the performance of simple models based on water-use efficiency ( $w$ ), defined as the ratio of biomass produced per unit water transpired, or radiation-use efficiency ( $e$ ), defined as biomass produced per unit of solar radiation intercepted. Water-use efficiency is typically estimated as  $w = K/D_a$ , where  $K$  is a parameter fitted empirically and  $D_a$  is the daytime vapor pressure deficit. The expectation is that  $e$  and  $K$  are conservative parameters that can be used across diverse climatic conditions. Experimental determination of  $K$  has been constrained by the need to measure crop transpiration, while the lack of consistency of the methodologies used in reported field experiments has limited the assessment of the transferability of both  $e$  and  $K$  values. A two-leaf hourly-time-step canopy transpiration and photosynthesis model (CTP) was formulated which after evaluation could be used to assess the transferability of these parameters across climatic conditions while eliminating experimental and biological variability. Model simulations of transpiration, tested on the basis of lysimetric data for wheat (*Triticum aestivum* L.) and maize (*Zea mays* L.), agreed well with the magnitude and time evolution of the data. Simulated values of  $w$  for wheat and maize in eight world locations with contrasting climatic conditions, plotted as a function of air vapor pressure deficit, were compared with experimental values from several other locations. Despite differences in cultivars, crop management, methods to estimate transpiration, sampling methods for biomass, and other sources of variability and experimental error in the available data, the agreement was adequate. These evaluations provide support to the use of the CTP model as a tool to assess the applicability of simple models of biomass production across climatic conditions.



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An increasing need to evaluate crop productivity under limited or uncertain water supply scenarios has renewed interest in simple models of crop productivity that can be readily applied to a large number of crop species across the range of climatic conditions where these crops are typically grown. Two such models have been widely utilized, one based on radiation-use efficiency ( $e$ ) (Warren-Wilson, 1967; Monteith, 1977) and the other on water-use efficiency ( $w$ ) (Bierhuizen and Slatyer, 1965).

$$\sum B = e \sum (Q^o f_i) \quad [1]$$

$$\sum B = \sum wT = K \sum (T / D_a) \quad [2]$$

where  $B$  is biomass,  $Q^o$  is incoming (above canopy) solar radiation,  $f_i$  is the fraction of incoming solar radiation intercepted by the canopy,  $T$  is transpiration, and  $K$  is a transpiration to biomass conversion coefficient, which divided by the daytime mean air vapor pressure deficit ( $D_a$ ) allows the estimation of  $w$ . Equations [1] and [2] are typically integrated using a daily time step. Tanner and Sinclair (1983) presented a derivation of Eq. [2] from principles and argued that the parameter  $K$  was conservative, providing a simple approach to calculate plant biomass production.

Although these models were introduced early in the 20th century, experimental determination of  $K$  and  $w$ , in particular, has been limited because of the need to measure crop transpiration, making it difficult to assess the transferability of these parameters among locations. The problem is compounded because an important fraction of the variability can be traced back to experiments with different crop varieties, crop management, methods of determination of transpiration rates, methods for biomass sampling, and other sources of variability (Sinclair and Muchow, 1999).

A properly evaluated mechanistic model of canopy transpiration and photosynthesis, which can be utilized to estimate  $e$ ,  $k$ , and  $w$ , would be useful to evaluate the transferability of these parameters across climatic conditions while eliminating experimental and biological variability. The formulation and evaluation of such a model is the subject of this paper. Specifically, the main objectives of the work reported here were (i) to present a canopy transpiration and photosyn-

thesis (CTP) model that can be used for simulation scenarios involving diverse climatic conditions, agricultural crops, and water stress conditions, (ii) to compare model simulations of crop transpiration with field data for wheat and maize, and (iii) to test the model's ability to simulate water-use efficiency by comparison with field data for wheat and maize.

The calculation of photosynthesis and transpiration is usually approached using either a single-layer, big-leaf model (e.g., Sellers et al., 1992; Dickinson et al., 1998; Tuzet et al., 2003) or a multilayer model (e.g., Leuning et al., 1995; Wang and Jarvis, 1990), including multiple classes of leaf inclination and azimuth classes per canopy layer (e.g., Stöckle, 1992). A few decades ago, Sinclair et al. (1976) discussed the advantages of using a two-leaf model to estimate photosynthesis by separately integrating the sunlit and shaded canopy fractions. This simplification is effective because photosynthesis in shaded leaves has a linear response to irradiance, whereas sunlit leaves are often light saturated, which allows the use of mean irradiance for each fraction carrying a modest error in the prediction of canopy photosynthesis (de Pury and Farquhar, 1997). The two-leaf approach has also been applied to the calculation of canopy transpiration (Fuchs et al., 1987; Stöckle, 1992; Petersen et al., 1992). Stöckle (1992) compared a single-layer, two-leaf model with a multilayer model with nine leaf inclination classes and nine leaf azimuth classes and reported departures as low as 0.5% and as high as 9%, with typical departures of 3 to 6% for canopy transpiration and photosynthesis. Models coupling stomatal conductance, transpiration, and photosynthesis that use a two-leaf approach have been introduced by Wang and Leuning (1998) and Dai et al. (2004); comparisons of these models with field data were presented by Leuning et al. (1998) and Dai et al. (2004).

The development of the two-leaf canopy transpiration and photosynthesis model presented here relied on available literature of canopy radiation, transpiration, and photosynthesis modeling, emphasizing the selection of methods based on measurable inputs and avoiding the leaf-to-canopy scaling problem by utilizing a big-leaf approach. The main features of the CTP model are (i) partitioning of the canopy in sunlit and shaded fractions, (ii) calculation of canopy solar radiation interception and average solar and photosynthetically active radiation (PAR) irradiance for sunlit and shaded leaves, (iii) computation of canopy transpiration for sunlit and shaded fractions using a big-leaf approach, (iv) calculation of photosynthesis for two "average leaves" representing the sunlit and shaded fractions of the canopy, (v) leaf photosynthesis calculated by balancing the biochemical capacity for CO<sub>2</sub> assimilation (demand) and the CO<sub>2</sub> flux from the bulk air (supply), (vi) average leaf stomatal conductance responsive to light, temperature, atmospheric CO<sub>2</sub> concentration, air vapor pressure deficit, and plant water



status, and (vii) simulation of plant water uptake and the effect of plant water stress on stomatal conductance.

The CTP model differs from the models of Wang and Leuning (1998) and Dai et al. (2004) in that the scaling from leaf to canopy is obviated by calculating a big-leaf energy balance for sunlit and shaded fractions to obtain canopy transpiration (e.g., Fuchs et al., 1987), which is generally comparable with the Penman-Monteith equation widely tested by practitioners evaluating water use by field-grown crops (Allen et al., 1998). Similarly, sunlit and shaded canopy photosynthesis are calculated for each big leaf by utilizing the mean PAR irradiance per unit leaf area and the leaf temperature derived from the energy balance of each fraction. Other differences include the treatment of stomatal conductance and the inclusion in CTP of a plant water uptake model considering plant hydraulic conductance, water potentials in the continuum soil-plant-atmosphere, and the relation between stomatal conductance and leaf water potential. No attempt was made to correct for canopy distribution of leaf canopy nitrogen. For canopies low in total nitrogen, daily assimilation rates are similar to 10% lower when leaf nitrogen is distributed uniformly than when the same total N is distributed according to an exponentially decreasing profile of absorbed radiation. However, this effect is negligible for plants with high N concentrations (Leuning et al., 1995).

## The CTP Model

A brief description of the CTP model will be presented here; readers should consult Kremer (2006) for more details on supporting equations and references. The model is available as a MS Excel file, with code embedded in the file using Visual Basic for Applications and Excel worksheets as interface for input and output operations. The model can be downloaded from [www.bsye.wsu.edu/cropsyst](http://www.bsye.wsu.edu/cropsyst); verified 2 June 2008.

The model utilizes an hourly time step of integration and includes dimensionless functions to estimate hourly climatic data from daily input data (Kremer, 2006). The simulation of canopy radiation is based on methods presented by Campbell and Norman (1998), which summarize calculation approaches developed by researchers in the last several decades. This includes the calculation of direct and diffuse components of short wave irradiance, transmission through the canopy of beam and diffuse components, global solar irradiance reflected and absorbed by the canopy, and global and PAR solar irradiance for an average sunlit and shaded leaf.

### Canopy Transpiration

The calculation of canopy transpiration, estimated as the sum of transpiration from the sunlit and shaded fractions of the canopy, is based on Fuchs et al. (1987), Allen et al. (1998), and Campbell and Norman (1998). For each fraction, transpiration is calculated by solving the canopy energy balance to obtain latent heat loss  $\lambda_v E_c$ , where  $\lambda_v$  is the latent heat of vaporization ( $\text{J kg}^{-1} \text{H}_2\text{O}$ ) and  $E_c$  is transpiration ( $\text{kg H}_2\text{O s}^{-1} \text{m}^{-2}$ ).

The canopy energy balance, assuming that heat storage and metabolic heat production are negligible, is given by:

$$S_{\text{abs}} - L_c - H - \lambda_v E_c = 0 \quad [3]$$

where  $S_{\text{abs}}$  is the radiation absorbed by the canopy,  $L_c$  is the emitted long wave radiation,  $H$  is the sensible heat, and  $\lambda_v E_c$  is the latent heat, all terms in  $\text{J s}^{-1} \text{m}^{-2}$ . All terms, except the first, have a dependency on the aerodynamic canopy temperature, whose value is found iteratively for each hourly time step. Heat and vapor conductance, vapor gradients, and other variables needed to calculate the terms are determined directly from weather inputs, while stomatal conductance to calculate latent heat requires iteration to satisfy transpiration and photosynthesis simultaneously.

The water vapor conductance for either the sunlit or shaded fraction of the canopy ( $g_v$ ) is the resultant of three conductances added in series: aerodynamic conductance ( $g_a$ ), boundary layer conductance to water vapor ( $g_{bv}$ ), and stomatal conductance to water vapor ( $g_{sv}$ ):

$$g_v = \frac{1}{\frac{1}{\left( \frac{g_{sv} g_{bv}}{g_{sv} + g_{bv}} \right) \text{LAI}} + \frac{1}{g_a}} \quad [4]$$

where the term including LAI is the water vapor conductance of a typical leaf integrated over the canopy green leaf area index (sunlit or shaded). The stomatal conductance to water vapor is estimated as  $g_{sv} = 1.56 g_s$ , where  $g_s$  is the stomatal conductance to  $\text{CO}_2$ .

The canopy heat conductance for either the sunlit or shaded fraction of the canopy ( $g_h$ ) is assessed as:

$$g_h = \frac{1}{\frac{1}{g_a} + \frac{1}{(g_{bh} \text{LAI})}} \quad [5]$$

where the product  $g_{bh}$  LAI is the heat boundary layer conductance of a typical leaf integrated over the canopy green leaf area index (sunlit or shaded) and  $g_{bh}$  is the boundary layer conductance for heat. The terms  $g_a$ ,  $g_{bv}$ , and  $g_{bh}$  are calculated as given by Campbell and Norman (1998).

### Canopy Net Photosynthesis

Canopy net photosynthesis is estimated by integration over the canopy leaf area of the net photosynthesis per unit sunlit and shaded leaf area. Leaf photosynthesis is computed balancing the biochemical capacity for  $CO_2$  assimilation (demand) and the  $CO_2$  flux from the bulk air to the intercellular spaces within the leaf (supply).

### Carbon Dioxide Demand

The models of leaf photosynthesis presented by Collatz et al. (1991) ( $C_3$  assimilation pathway) and Collatz et al. (1992) ( $C_4$  assimilation pathway) were adopted for the calculation of net assimilation ( $A_n$ ). Net assimilation is computed as the minimum of three potential  $CO_2$  uptake rate capacities: light-limited rate ( $J_E$ ), Rubisco-limited rate ( $J_R$ ), and either the rate imposed by sucrose synthesis ( $J_S$ ,  $C_3$  plants) or the  $CO_2$ -limited rate ( $J_C$ ,  $C_4$  plants), all rates in  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .

$$A_n = \min \{ J_E, J_R, J_S, \text{ or } J_C \} - R_d \quad [6]$$

where  $R_d$  symbolizes the cost of the leaf photosynthesis as “day” respiration rate.

For the  $C_3$  assimilation pathway,  $J_E$  is given by:

$$J_E = \frac{\alpha \delta R (C_i - \Gamma^*)}{C_i + 2\Gamma^*} \quad [7]$$

where  $\alpha$  is the leaf PAR absorptivity,  $\delta$  is the intrinsic quantum efficiency for  $CO_2$  uptake ( $\text{mol mol}^{-1}$ , maximum number of  $CO_2$  molecules fixed per quantum of radiation absorbed),  $R$  is the PAR flux density irradiance on the leaf in ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $C_i$  is the intercellular  $CO_2$  concentration ( $\mu\text{mol mol}^{-1}$ ), and  $\Gamma^*$  is the light compensation point, which is calculated as:

$$\Gamma^* = \frac{C_o}{2\omega} \quad [8]$$

where  $C_o$  is the oxygen concentration in air ( $210 \text{ mmol mol}^{-1}$ ), and  $\omega$  is a ratio describing the portioning of the carboxylase and oxygenase reactions of Rubisco.

The Rubisco-limited assimilation rate is calculated as:

$$J_R = \frac{V_m (C_i - \Gamma^*)}{C_i + K_c \left( 1 + \frac{C_o}{K_o} \right)} \quad [9]$$

where  $V_m$  is the maximum Rubisco capacity per unit area ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $K_o$  ( $\text{mmol mol}^{-1}$ ) and  $K_c$  ( $\mu\text{mol mol}^{-1}$ ) are the Michaelis–Menten constants for  $\text{O}_2$  and  $\text{CO}_2$ . When the concentration of photosynthesis products raises and the use and export of these products are limited, a slower reaction is imposed. This effect is accounted through the sucrose synthesis rate:

$$J_S = \frac{V_m}{2} \quad [10]$$

Equations [7], [9], and [10] imply a sharp transition from one rate limiting process to another. In reality, there is a more gradual transition with some colimitation when two rates are nearly equal. This gradual transition is modeled empirically using quadratic functions (Collatz et al., 1991).

The rate of respiration is estimated as  $R_d = 0.015 V_m$ . Temperature effects on photosynthesis are accounted through temperature adjustments of the parameters  $V_m$ ,  $R_d$ ,  $K_c$ ,  $\omega$ , and  $K_o$ .

Collatz et al. (1992) proposed a simplified model to estimated leaf net photosynthesis for  $\text{C}_4$  assimilation pathway. These authors hypothesized that the light-limited rate of photosynthesis, under conditions where the partial pressure of  $\text{CO}_2$  in the bundle sheath chloroplast is sufficiently high to suppress photorespiration is given by

$$J_E = \alpha \delta \gamma R \quad [11]$$

where  $\alpha$  is the absorptivity of the leaf for PAR,  $\delta$  is the intrinsic quantum efficiency for  $\text{CO}_2$  uptake ( $\text{mol mol}^{-1}$ ),  $R$  is the PAR flux density irradiance on the leaf in ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and,  $\gamma$  is the fraction of absorbed  $R$  that is used for production of Rubisco.

The  $\text{CO}_2$ -limited rate is given by

$$J_C = \mu C_i \quad [12]$$

where  $\mu$  is the slope of the  $\text{CO}_2$  ( $\text{mol m}^{-2} \text{s}^{-1}$ ) responses curve at low internal  $\text{CO}_2$ . When the rate of assimilation is not limited by light and  $\text{CO}_2$ , the rate is instead defined by the capacity of Rubisco to attach  $\text{CO}_2$ . Under these conditions, the concentration of  $\text{CO}_2$  on the bundle sheath chloroplast nearly saturates Rubisco activity, and then

$$J_R = V_m \quad [13]$$

Respiration, colimitations, and net photosynthesis are determined similarly as explained for the  $\text{C}_3$ . The parameters  $V_m$  and  $\mu$  are adjusted by temperature.



To calculate temperature adjustments to  $C_3$  and  $C_4$  photosynthesis, leaf temperature is computed as the temperature that closes the energy balance for an average sunlit or shaded unit leaf area using the approach suggested by Campbell and Norman (1998).

### Carbon Dioxide Supply

The  $CO_2$  gas exchange between the atmosphere and the intercellular spaces of the leaf is described by Fick's law:

$$A_n = g_{tc} (C_a - C_i) \quad [14]$$

where  $g_{tc}$  is the total conductance for  $CO_2$  ( $\text{mol m}^{-2} \text{s}^{-1}$ ),  $C_a$  is the atmospheric  $CO_2$  concentration ( $\mu\text{mol mol}^{-1}$ ), and  $C_i$  is the leaf intercellular  $CO_2$  concentration ( $\mu\text{mol mol}^{-1}$ ). The value of  $C_i$  is obtained through iteration until equilibrium between  $CO_2$  demand and supply is reached. The total conductance for  $CO_2$  includes three conductances in series: aerodynamic conductance ( $g_a$ ), boundary layer  $CO_2$  conductance ( $g_{bc}$ ), and stomatal  $CO_2$  conductance ( $g_s$ ).

### Stomatal Carbon Dioxide Conductance

The calculation of  $g_s$  is essential in the simulation of crop productivity, affecting both photosynthesis and transpiration (Yu et al., 2004). Jarvis (1976) developed an empirical model to predict stomatal conductance using the maximum stomatal conductance ( $g_s^{\max}$ ) for the plant species multiplied by non interactive correction coefficients representing the independent effect of solar irradiance ( $f_s$ ), leaf temperature ( $f_T$ ), air vapor pressure deficit ( $f_{Da}$ ), atmospheric  $CO_2$  concentration ( $f_{Ca}$ ), and leaf water potential ( $f_{\psi l}$ ).

$$g_s = g_s^{\max} f_s f_T f_{Da} f_{Ca} f_{\psi l} \quad [15]$$

Another semi-empirical model was presented by Ball et al. (1987) and based on previous concepts by Wong et al. (1979). Wong et al. (1985a, 1985b, 1985c) partitioned the responses of stomata to changes in the environment into components that are dependent on photosynthesis and others that are independent of photosynthesis

$$g_s = b + m \frac{A_n h_s}{C_s} \quad [16]$$

where  $A_n$  is the leaf net photosynthesis rate,  $h_s$  is relative humidity, and  $C_s$  is the  $CO_2$  concentration of air at the leaf surface. The parameters  $m$  and  $b$  are the slope and intercept of a linear regression that must be determined empirically.

Equation [16] can be redefined by replacing the effects of the relative humidity with a hyperbolic function of humidity deficit ( $f_{Dl}$ ) (Leuning, 1995), introducing a

water stress function ( $f_w$ ), and assuming that  $b$  is negligible (typically, a very low value compared with the  $g_s$  of leaves actively assimilating  $\text{CO}_2$ ), yielding the following form:

$$g_s = m \frac{A}{C_s} f_{D1} f_w \quad [17]$$

and  $f_{D1}$  defined as

$$f_{D1} = \frac{g_{D1}^0}{g_s^{\max} (1 + D_1/D_o)}; \text{ if } f_{D1} > 1, \text{ then } f_{D1} = 1 \quad [18]$$

where  $D_1$  is the leaf to air vapor pressure difference, and  $g_{D1}^0$  and  $D_o$  are fitted parameters. For a given atmospheric  $\text{CO}_2$  concentration, a maximum value of  $g_s$  ( $g_s^{\max}$ ) can be observed for the following condition: no water stress ( $f_w \approx 1$ ), photosynthesis operating at optimum light and temperature ( $A_n^*$ ), and low vapor pressure deficit ( $f_{D1} \approx 1$ ). Under this condition, Eq. [16] can be written as

$$g_s^{\max} = m \frac{A_n^*}{C_s} \quad [19]$$

Thus, a relative stomatal conductance is obtained by dividing Eq. [17] by Eq. [19].

$$\frac{g_s}{g_s^{\max}} = \frac{A_n}{A_n^*} f_{D1} f_w \quad [20]$$

Rearranging Eq. [20], a model with physiological relationships similar to the Ball et al. (1987) model but introducing the effects of plant water stress and humidity as presented by Jarvis (1976) is obtained

$$g_s = g_s^{\max} f_{D1} f_w \frac{A_n}{A_n^*} \quad [21]$$

Equation [21] requires  $g_s^{\max}$ , which is well documented for many crops (e.g., Körner et al., 1979; Körner, 1994; Kelliher et al., 1995; Monteith, 1995). However,  $g_s^{\max}$  is also dependent on atmospheric  $\text{CO}_2$  concentration. Therefore, a  $\text{CO}_2$  adjustment factor ( $f_{\text{CO}_2}$ ) was added to Eq. [21].

$$g_s = g_s^{\max} f_{\text{CO}_2} f_{D1} f_w \frac{A_n}{A_n^*} \quad [22]$$

with the  $\text{CO}_2$  adjustment factor expressed as

$$f_{\text{CO}_2} = 1 - (C_a - C_a^{\text{ref}}) S_{\text{CO}_2} \quad [23]$$

where  $C_a^{\text{ref}}$  is the reference atmospheric  $\text{CO}_2$  (atmospheric  $\text{CO}_2$  concentration at the time when  $g_s^{\max}$  was observed), and  $S_{\text{CO}_2}$  is a sensitivity constant ( $0.0012 \text{ mol m}^{-2} \text{ s}^{-1}$

stomatal conductance change per  $\mu\text{mol mol}^{-1}$  change in atmospheric  $\text{CO}_2$  concentration), adapted from Morison (1987).

The water stress function ( $f_w$ ) adjusts maximum stomatal conductance as a function of leaf water potential (Fischer et al., 1981; Jones, 1992):

$$f_w = \frac{1}{1 + (\bar{\psi}_1 / \psi_{1/2})^n} \quad [24]$$

where  $\bar{\psi}_1$  is the mean leaf water potential ( $\text{J kg}^{-1}$ ) either for sunlit or shaded leaves,  $\psi_{1/2}$  is the value of  $\bar{\psi}_1$  ( $\text{J kg}^{-1}$ ) when  $g_s$  is half of the maximum, and  $n$  is a fitted coefficient. The mean leaf water potential is determined by the equilibrium between water uptake from the root zone and water loss as transpiration (Stöckle and Jara, 1998).

### Iterative Solution

Given the interactions (shared variables) between canopy transpiration, leaf and canopy temperature, photosynthesis, stomatal conductance, and plant water uptake, the equations describing these processes were solved through nested iterative procedures until equilibrium solutions were found for the sunlit and shaded canopy fractions in each simulation time step (1 h). Figure 6-1 shows a diagram of the iterative solution procedure.

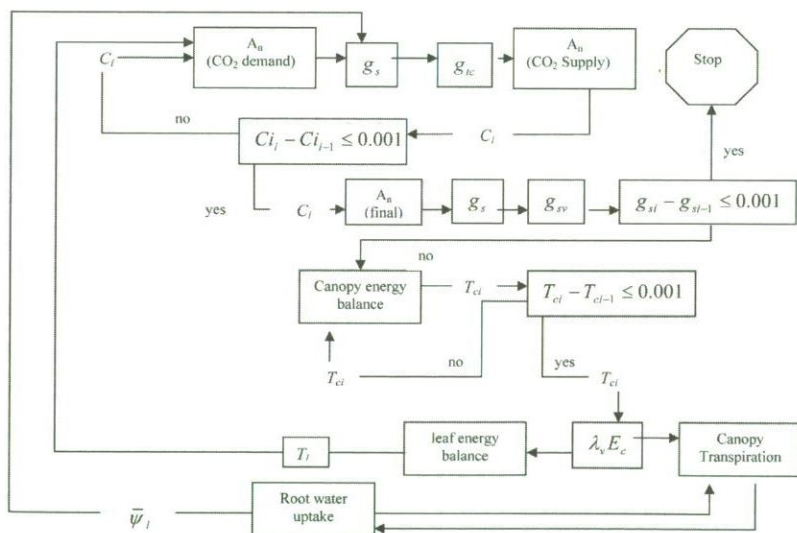


Fig. 6-1. Model diagram of main equations and their iterative solution, where  $A_n$  is the leaf net photosynthesis,  $T_c$  and  $T_l$  are canopy and leaf temperature,  $g_s$ ,  $g_{sc}$ , and  $g_{sw}$  are the average leaf stomatal conductance for  $\text{CO}_2$ , leaf conductance to  $\text{CO}_2$  and water vapor,  $\bar{\psi}_1$  is the average leaf water potential,  $\lambda_v E_c$  is the canopy latent heat,  $i$  is an index indicating time step, and  $C_i$  is the internal  $\text{CO}_2$ .

Table 6-1. List of input parameters used for model simulations.

Parameters	Units	Maize	Wheat	Equation number
$K_c$	$\mu\text{mol mol}^{-1}$		237	9
$K_o$	$\mu\text{mol mol}^{-1}$		328	9
$\delta$	$\mu\text{mol mol}^{-1}$		0.08	7
$V_m$	$\mu\text{mol m}^{-2} \text{s}^{-1}$	51.5	135	9, 13
$u$	$\text{mol m}^{-2} \text{s}^{-1}$	1.038		12
$\delta\gamma$	—	0.067		11
$\delta_{DI}^0$	$\text{mol m}^{-2} \text{s}^{-1}$	0.87	2.31	18
$D_o$	kPa	0.66	0.40	18
$g_s^{\text{max}}$	$\text{mol m}^{-2} \text{s}^{-1}$	0.4	0.5	21
$\psi_{1/2}$	$\text{J kg}^{-1}$	-1660	-1600	24
$n$	—	7	10	24

## Material and Methods

### Parameterization of the Model for Wheat and Maize

Input parameter values used for the simulation of wheat and maize transpiration and photosynthesis are given in Table 6-1. Additional information is available in Kremer (2006).

### Evaluation of Model Simulation of Crop Transpiration

The CTP model was evaluated using climatic and crop data from the Conservation and Production Research Laboratory, Bushland, TX (35°11' N, 102°06' W; elevation 1170 m above mean sea level). Crop information including daily LAI, evapotranspiration, crop height, and aboveground biomass production for wheat (*Triticum aestivum*; 1989–1990, 1991–1992, and 1992–1993 growing seasons) and maize (*Zea mays*; 1990 growing season and Pioneer 3245; 1994 growing season) were available. The data selected encompassed the period starting after the crop reached a green LAI of 2.5 and ending just days after the beginning of canopy senescence. Crop evapotranspiration was extracted for daily periods between 0700 and 1900 h from lysimetric measurements. These data came from two groups of two adjacent lysimeters identified as North east (NE) and South east (SE) for wheat (1991–1992) and maize (1990) and North west, (NW) and South west (SW) for wheat (1989–1990; 1992–1993). For maize 1994, only a single lysimeter data was utilized (SE). These data were selected because they presented complete climatic record and crop information. Daily weather data included global irradiance, mean wind velocity, and maximum and minimum air temperature and relative



humidity, recorded by instruments adjacent to each lysimeter, deployed over the same crop as in the lysimeter.

Crop transpiration ( $T$ ) was calculated from crop evapotranspiration by assuming that  $T$  is proportional to the fraction of solar irradiance intercepted by the canopy.

$$T = ET(1 - \tau_{bt}) \quad [25]$$

where  $T$  is crop transpiration ( $\text{kg m}^{-2}$ ),  $ET$  is the lysimeter evapotranspiration ( $\text{kg m}^{-2}$ ) and  $\tau_{bt}$  is the fraction of incident solar irradiance that penetrates the canopy and reaches the soil surface. The crops were well watered and no water stress was documented.

The agreement between simulations and observations of crop transpiration was evaluated on the basis of graphical and statistical methods. Statistical indices included the Willmott index of agreement (Willmott, 1981), the root mean square error (RMSE), the mean absolute error, and the coefficient of residual mass (Loague and Green, 1991).

## Evaluation of Model Simulation of Water-Use Efficiency

### Experimental Data

Experimental data suitable for the calculation of  $w$  for crops growing without water shortage were obtained from published articles and direct communication with selected researchers. In a few instances, experimental  $w$  values were readily available, but in most cases, they were derived from raw data. The quality of the available data differed and was classified as follows: (a) complete data set available including daily crop transpiration, crop above ground biomass accumulation and LAI determined at reasonably frequent intervals, and daily measurements of global solar radiation, air temperature, air relative humidity and wind speed; (b) daily crop transpiration or evapotranspiration was not reported; (c) data set includes daily crop evapotranspiration but not transpiration; and (d) crop transpiration and biomass are presented as total for the period, and  $D_a$  is averaged for the same period. For type (a),  $w$  was readily calculated; for type (b), daily crop transpiration was simulated using the CTP model; for type (c), crop transpiration was computed as in Eq. [25], with the fraction of intercepted solar radiation estimated from LAI; and for type (d), a seasonal value of  $w$  was readily calculated. Daytime  $D_a$  was computed as 2/3 of the maximum  $D_a$  for each day (e.g., Kemanian et al., 2005), the latter determined from maximum temperature and minimum relative humidity. Daily ETo calculations were performed as proposed by Allen et al. (1998).

Tables 6–2 and 6–3 summarize the available data and their quality type.

**Table 6–2. Wheat water-use efficiency ( $w$ ) and  $k$  reported or calculated from literature data.  $Q$  refers to the quality of the data as described in the text.**

Source†	Site	Q	Variety	$w$ g kg <sup>-1</sup>	$k$ Pa	$D_a$ kPa	Observations
(1)	Mederrin, Australia	d	Gutha	4.61	4.43	0.96	1987
			Gameny	4.49	4.67	0.96	
			Purple Straw	3.95	4.11	0.96	
(2)		d	Timgalen	5.00	4.08	0.82	1973, D1, preanthesis
				4.30	5.10	1.19	1973, D1, postanthesis
				4.90	4.50	0.92	1973, D2, preanthesis
				3.90	4.80	1.23	1973, D2, postanthesis
				3.60	3.87	1.07	1973, D3, preanthesis
				3.10	4.20	1.35	1973, D3, postanthesis
				4.20	3.81	0.91	1975, D1, preanthesis
				4.10	4.80	1.17	1975, D1, postanthesis
				3.40	3.33	0.98	1975, D2, preanthesis
				3.40	4.73	1.39	1975, D2, postanthesis
(3)	Werribee, Australia	d	Bank	6.60	4.74	0.7	1984
				7.53	4.82	0.64	1985
			Quarrion	7.24	4.93	0.68	1984
				8.61	5.26	0.61	1985
(4)	Moombooldool, Australia	a	Gutha	7.10	3.80	0.54	1985, preanthesis
			Quarrion	5.87	4.79	0.71	
(5)	Toowoomba, Australia	d	Hartog	3.93	4.58	1.18	1993
(6)	Nottinghamshire, UK	d	Soissons	5.29	3.44	0.6	1994
				5.77	3.75	0.63	1995
			Maris Huntsman	6.20	4.03	0.60	1994
				6.22	4.04	0.63	1995
(7)	Pullman, WA	a	WB926R	4.59	5.90	1.13	Pooling 1998/1999
(8)	Bushland, TX	c		5.10	5.30	1.21	1989–1990
				3.94	4.63	1.01	1991–1993 NE Lysimeter
				3.59	4.32	0.95	1991–1992 SE Lysimeter
				3.94	4.00	1.04	1992/93 NW Lysimeter
				4.38	4.55	1.02	1992–1993 SW Lysimeter
(9)	Aleppo, Syria	b	Cham1	4.45	5.53	1.32	1990
			Huarina	4.64	6.00	1.32	1990
(10)	Pucawan, Australia	d	Average of	6.20	3.43	0.51	preanthesis, low N
			Cometz,	5.20	2.70	0.51	preanthesis, high N
			Janz and	3.74	5.83	1.54	postanthesis, low N
			Kulin	3.39	5.22	1.54	postanthesis, high N

† (1) Siddique et al. (1990),  $D_a$  from Siddique et al. (2) Doyle and Fischer (1979); (3) Connor et al. (1992); (4) Condon et al. (1993); (5) Meinke et al. (1997); (6) Foulkes et al. (2001); (7) Marcos (2000); (8) Howell, T. (personal communication) (9) Pala et al. (1996); (10) Angus and van Herwaarden (2001).

**Table 6–3. Maize water-use efficiency ( $w$ ) and  $k$  reported or calculated from literature data. Q refers to the quality of the data as described in the text.**

Source†	Site	Q	Variety	$w$ g kg <sup>-1</sup>	$k_{Da}$ Pa	$D_a$ kPa	Observations
(1)	Logan, UT	d	Utahybrid <sup>±</sup> 544a and NKPX–20	4.12	8.4	2.04	1974–1975
	Ft. Collins, CO	d	NKPX–20 and Pioneer 3955	4.88	10.2	2.09	1974–1975
	Davis, CA	d	Funks 4444	4.93	9.9	2.01	1974–1975
(2)	Elora, ON, Canada	d	PAG SXIII	6.12	6.06	0.99	1981– low density
				8.25	8.16	0.99	1981–high density
				6.64	6.93	1.04	1982–high N
				7.44	7.55	1.02	1982–low N
(3)	Davis, CA	c		5.14	9.92	2.04	1974
(4)	Prosser, WA	b		6.01	9.90	1.68	2004–early seeding
				6.3	8.85	1.6	2004–late seeding
(5)	Bushland, TX	c	Pioneer 3124	6.56	8.58	1.42	1990 NE Lysimeter
			Pioneer 3245	5.69	8.81	1.7	1990 SE Lysimeter
			Pioneer 3245	5.21	6.88	1.38	1994 NW Lysimeter
(6)	Lebanon, Bekaa Valley	d	Manuel	4.18	13.83	3.31	1998

† (1) Ehlers and Goss (2003), extracted from Tanner and Sinclair (1983); (2) Walker (1986); (3) Acevedo (1975); (4) Kremer (2004, not published); (5) Howell, T. (personal communication); (6) Karam et al. (2003).

‡ The mention of trade names of commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation or endorsement by either the University of Chile, Washington State University, Texas Agricultural Experiment Station, or the U.S. Department of Agriculture.

### Simulations and Calculations

The water-use efficiency values summarized in Tables 6–2 and 6–3 are seasonal (not daily) values, and corresponding daily weather data are seldom available, making them difficult to compare with the daily  $w$  values simulated by CTP.

Thus, for model evaluation, an indirect approach was used, where  $w$  values for wheat and maize were simulated for a wide range of climatic conditions and compared with the available data by plotting in the same graph experimental and simulated  $w$  values as a function of  $D_a$ .

To generate diverse climatic conditions for the simulation of  $w$  for wheat and maize, daily weather data from eight world locations were selected. The data were composed of daily measurements of global solar radiation (MJ m<sup>-2</sup> d<sup>-1</sup>), maximum and minimum air temperature (°C), maximum and minimum air relative humidity, and average wind speed at 2-m height (m s<sup>-1</sup>), encompassing a period of 4 mo starting on May and November for the northern and southern hemisphere, respectively. Data were for a year selected at random in the following locations: Concepcion del Uruguay (Argentina, 32°28' S, 58°16' W; elevation 20 m), Landriano (Italy, 45°18' N, 9°15' E; elevation 78 m), Temple (TX, USA; 31° 7' N, 97°4' W;

**Table 6-4.** Average maximum and minimum temperature ( $T_x$ ,  $T_n$ ), solar radiation ( $S_i$ ), maximum and minimum relative humidity ( $RH_x$ ,  $RH_n$ ), wind speed (WS), reference evapotranspiration ( $ET_o$ ), and daytime vapor pressure deficit ( $D_a$ ) for eight locations and selected periods of 4 mo starting on May and November in the northern and southern hemisphere, respectively.

	$T_x$	$T_n$	$S_i$	$RH_x$	$RH_n$	WS	$ET_o$	$D_a$
	— °C —		MJ m <sup>-2</sup> d <sup>-1</sup>			m s <sup>-1</sup>	mm d <sup>-1</sup>	kPa
Concepción	27.8	16.9	21.5	0.99	0.65	3.0	4.3	0.8
Landriano	26.0	14.2	22.5	0.86	0.47	1.2	4.3	1.0
Temple	31.2	20.6	21.1	0.92	0.48	2.7	5.3	1.5
Pullman	22.6	8.4	23.3	0.81	0.33	2.1	4.4	1.1
Prosser	27.0	9.3	25.7	0.62	0.43	1.5	4.8	1.3
Ankara	27.9	14.3	21.1	0.63	0.32	1.8	5.0	1.8
Aleppo	34.7	17.5	27.2	0.67	0.26	4.8	9.0	2.6
Maricopa	38.9	24.3	27.6	0.79	0.25	2.2	7.7	3.2

elevation 208 m), Pullman (WA, USA, 46°45' N, 117°1' W; elevation 756 m), Prosser (WA, USA, 46°N, 119°7' W; elevation 380 m), Ankara (Turkey, 40°7' N, 32°59' E; elevation 948 m), Aleppo (Syria, 36°1' N, 37°18' E; elevation 430 m) and DOY 166 through 239 for Maricopa (AZ, USA, 33°49' N, 112°1' W; elevation 359 m). The main climatic characteristics of the selected period in the eight locations are presented in Table 6-4.

Daily transpiration and photosynthesis for wheat and maize were simulated for all locations using the CTP model assuming well-watered and unstressed crops (similar to the criteria used to select the experimental  $w$  data). Soil water content (field capacity), LAI (= 4), crop height (= 1 and 2.5 m for wheat and maize, respectively), and crop parameters for photosynthesis and stomatal conductance were held constant during the entire simulation period and were the same at all locations. Thus, only daily weather was variable. To obtain  $w$  values integrated over several days and more amenable to comparison with the seasonal experimental values,  $w$  was averaged for moving 15-d intervals, shifted by 5 d throughout the 120-d period at each location.

The CTP model provides canopy net photosynthesis (kg CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>), which was converted to equivalent aboveground biomass by subtracting respiration and making appropriate conversion of carbon dioxide to glucose, and then partitioning glucose into top and root biomass. Growth respiration was accounted for using the energy cost of the biochemical pathway as proposed by Vertregt and Penning de Vries (1987). Maintenance respiration was determined as summarized by Norman and Arkebauer (1991), who calculated respiration rates (g glucose per g of biomass) for stems and roots (maintenance respiration of leaves assumed to be included in net photosynthesis) with temperature response given by a  $Q_{10}$  of 2. The root/shoot ratio was assumed as 0.45, which accounts for root



structural growth, autotrophic respiration, and rhizodeposition (Amos and Walters, 2006; Baker et al., 2007).

## Results and Discussion

### Canopy Transpiration

Daily simulated and observed canopy transpiration is presented in Fig. 6-2 and 6-3 for wheat and maize simulations. The figures show a good agreement between simulated and observed canopy transpiration with the model tracking well the daily fluctuations. The good performance of the model is also supported by statistical indices (Table 6-5). The RMSE, MAE, and D for wheat ranged from 0.17 to 0.26 mm d<sup>-1</sup>, 0.13 mm d<sup>-1</sup> to 0.20 mm d<sup>-1</sup>, and 0.90 to 0.93, respectively; whereas, for maize these indices ranged from 0.11 to 0.18 mm d<sup>-1</sup>, 0.09 to 0.16 mm d<sup>-1</sup>, and 0.90 to 0.93, respectively. There was a slight tendency to underestimate transpiration for wheat and maize, results supported by the sign of the of CRM index.

Four sources of error could explain some of the differences: (i) parameters are not specific for the varieties tested, (ii) field measurement errors, (iii) accuracy in the methodology used to transform the lysimetric evapotranspiration data to transpiration, and (iv) inaccuracies in the transformation of daily to hourly weather data.

### Water-Use Efficiency

Simulated  $w$  values for eight locations (Table 6-4) and observed values for available field experiments (Table 6-2 and 6-3) are plotted as a function of  $D_a$  in Fig. 6-4.

Experimental  $w$  data for wheat and maize are highly variable, which is partially a reflection of differences in experimental methods, cultivar, and management differences and plain experimental variability. Simulated values are also variable but less so, reflecting the differential effect on transpiration and photosynthesis of the interaction between weather conditions and canopy function. There was, however, a general, good agreement in the trend of the experimental and simulated data distribution as a function of  $D_a$ . These results seem to provide validity to the use of the CTP model in the evaluation of the transferability of parameters of simple models of biomass production.

A power function fit the simulated  $w$  data as a function of  $D_a$  for wheat ( $w = 4.78 D_a^{-0.57}$ ;  $r^2 = 0.93$   $n = 36$ ) and maize ( $w = 7.44 D_a^{-0.42}$ ;  $r^2 = 0.91$ ,  $n = 14$ ). These functions give  $w$  values of 7.1 and 10.0 g kg<sup>-1</sup> for wheat and maize at  $D_a = 0.5$  kPa, respectively, and 2.8 and 5.1 g kg<sup>-1</sup> at  $D_a = 2.5$  kPa. Considering that  $k = w D_a$  (from Eq. [2]), the functions can be modified to obtain values of  $K$  for wheat ( $k = 4.78 D_a^{0.43}$ ) and maize ( $k = 7.44 D_a^{0.58}$ ), which give  $K$  values of 3.5 and 5.0 Pa for wheat

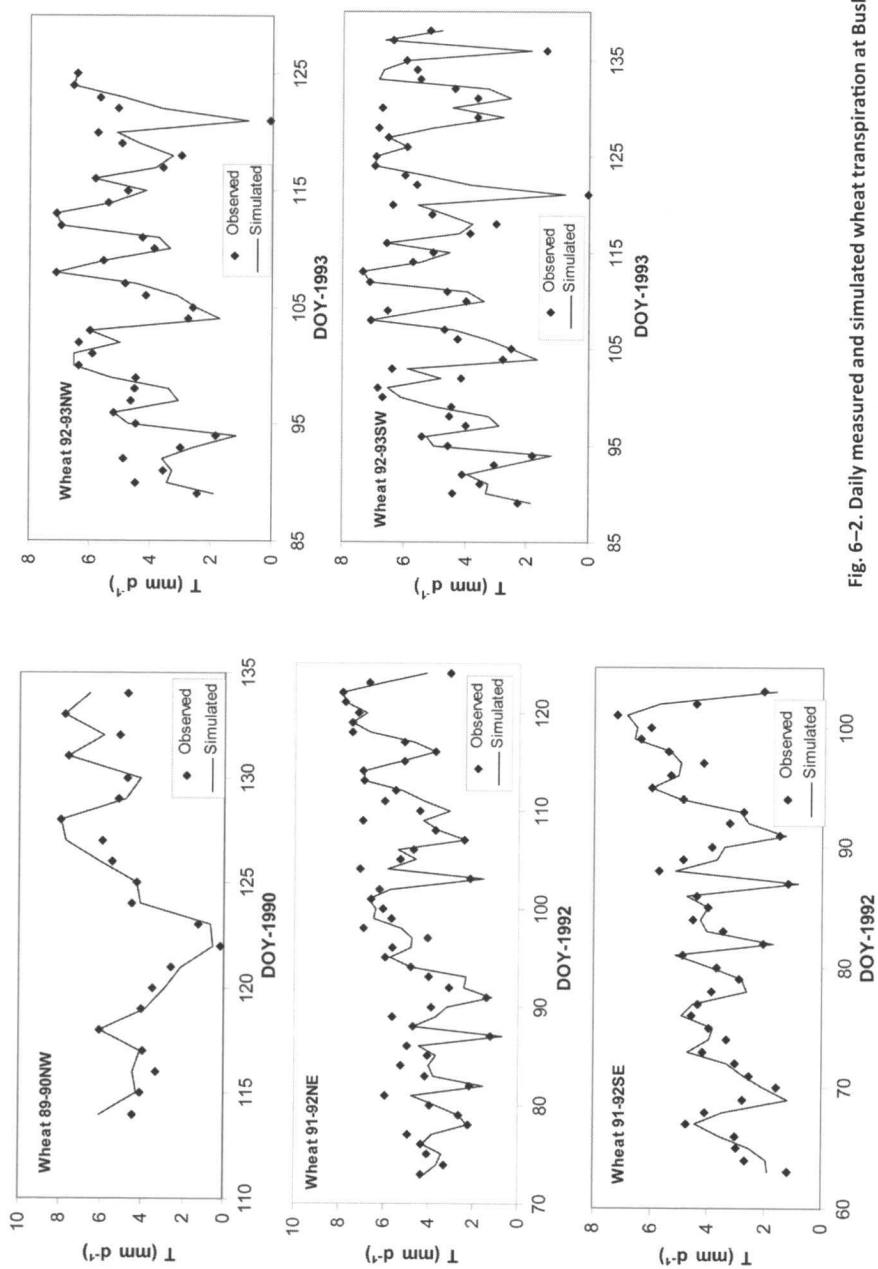


Fig. 6-2. Daily measured and simulated wheat transpiration at Bushland, TX, USA.

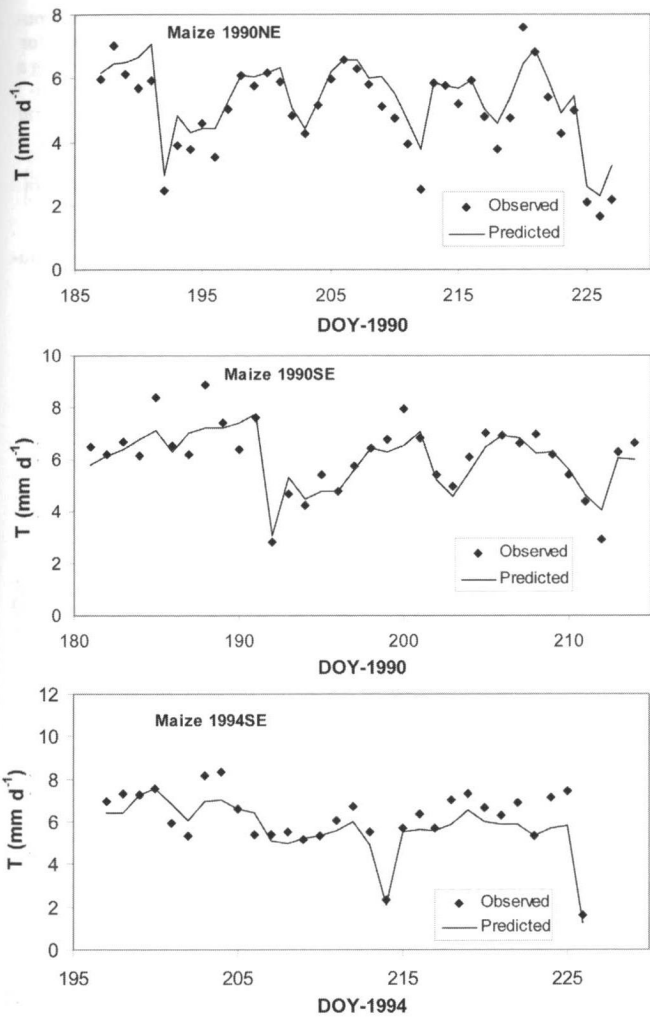


Fig. 6–3. Daily observed and simulated maize transpiration at Bushland, TX, USA.

Table 6–5. Statistical indexes of agreement between observed and simulated canopy transpiration of wheat and maize grown in Bushland, TX.

Crop	RMSE	MAE	<i>D</i>	CRM
	mm d <sup>−1</sup>			
Wheat 1989–1990NE	0.226	0.176	0.926	−0.080
Wheat 1991–1992NE	0.190	0.143	0.919	0.104
Wheat 1991–1992SE	0.148	0.117	0.918	0.012
Wheat 1992–1993NW	0.173	0.142	0.931	0.096
Wheat 1992–1993SW	0.191	0.159	0.919	0.089
Maize 1990NE	0.130	0.111	0.941	−0.090
Maize 1990SE	0.107	0.084	0.923	0.023
Maize 1994SE	0.143	0.124	0.904	0.088

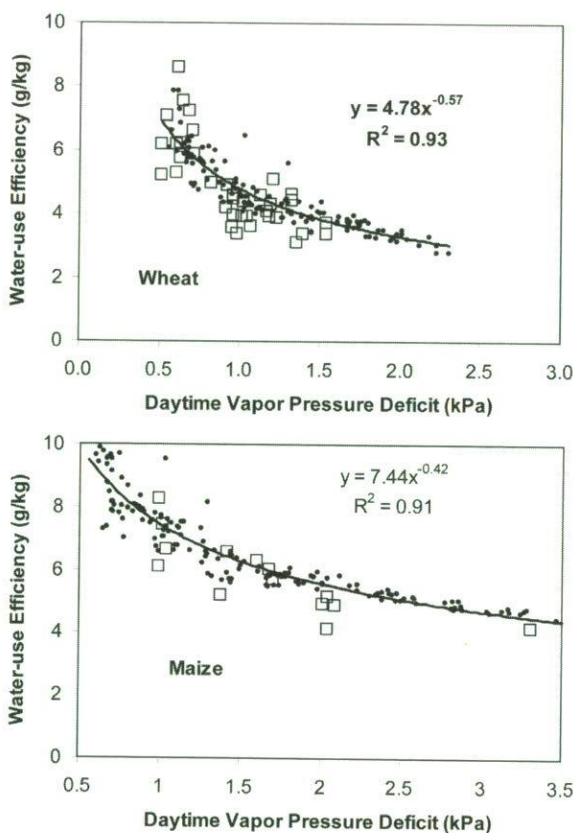


Fig. 6-4. Comparison of simulated water-use efficiency for eight locations representing a wide array of climatic conditions (dots) and experimental values for wheat and maize (squares) plotted as a function of  $D_a$ . Experimental data is described in Tables 6-2 (wheat) and 6-3 (maize). Equations were fitted to simulated values.

and maize at  $D_a = 0.5$  kPa, respectively, and 7.1 and 12.7 Pa at  $D_a = 2.5$  kPa. These  $K$  values are in agreement with the range of variation of available data. Figure 6-5 shows selected experimental  $K$  values from Tables 6-1 and 6-2 that were determined using daily integration of biomass, transpiration, and  $D_a$  (square symbols), compared with  $K$  values determined using the power functions for wheat and maize from CTP simulations (lines). The CTP model simulated  $K$  values that are within the range of observed variation and follow a similar relation with  $D_a$ .

In addition to providing support to the use of the CTP model as a tool to estimate water-use efficiency of crops on the basis of canopy radiation, photosynthesis, and transpiration parameterization, the results obtained support the view advanced by Kemanian et al. (2005) that the use of a constant  $K$  coefficient to determine water-use efficiency (Eq. [2]) is not granted. Earlier, de Wit (1958) suggested that a power function could appropriately represent the response of  $w$  to atmospheric water demand. Although the use of a seasonal  $K$  value could be useful for a generalized estimation of water productivity as proposed by Tanner



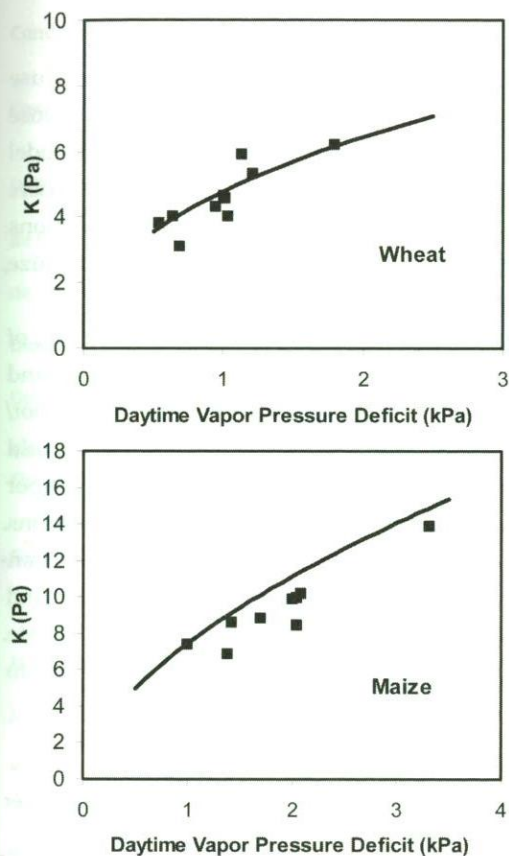


Fig. 6–5. Comparison of  $K$  values (Eq. [2]) determined using power functions obtained from CTP model simulations (see text for details) for eight locations representing a wide array of climatic conditions (lines) and selected experimental values (squares) from Tables 6–2 and 6–3 for wheat and maize, respectively.

and Sinclair (1983), this approach is not adequate for a detailed simulation of the evolution of biomass production in a given location and may produce important errors when a  $K$  constant determined experimentally in one location is used in another with different vapor pressure deficit.

Given the limitation of the Tanner and Sinclair approach, the best course of action is to determine  $w$  directly as a power function of vapor pressure deficit (Fig. 6–4). Well-controlled experiments at low, medium, and high values of daytime vapor pressure deficit in combination with a carefully parameterized CTP model can be used to obtain  $w$  vs.  $D_a$  functions for the main agronomic crops of interest.

This article is concerned with the description and evaluation of a two-leaf canopy photosynthesis and transpiration model suitable for the calculation of water-use efficiency and radiation-use efficiency of crops. The model evaluation and discussion presented herein has centered on well-watered crops, while the model performance under water stress conditions remains to be addressed. Some information is given by Stöckle et al. (2008) in this volume.

## Conclusions

The two-leaf CTP model's performance appeared adequate, supporting its use to calculate photosynthesis and transpiration of crop canopies with the purpose of determining water-use efficiency and radiation-use efficiency. The CTP model requires specialized but relatively easy-to-obtain input parameters and offers a wide range of applicability including different crops and weather conditions. Model simulations of transpiration, tested using field data for wheat and maize, showed good agreement with the time evolution of the observed data.

The model calculates water-use efficiency ( $w$ ) as kg of CO<sub>2</sub> fixed per kg of water transpired. This information was converted to kilograms of aboveground biomass per kilogram of water transpired by accounting for respiration and root/shoot partitioning. Simulated values of  $w$  for wheat and maize in eight world locations with contrasting climatic conditions, plotted as a function of air vapor pressure deficit, were compared with observed data from several other locations. Despite, differences in cultivars, crop management, methods to estimate transpiration, sampling methods for biomass, and other sources of variability and experimental error of the available observed data, the agreement was adequate. Further model evaluation with a larger number of crops would be desirable to extent the range of application.

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